Spanning the rich spectrum of the human brain: slow waves to gamma and beyond.

Sarang S. Dalal, Juan R. Vidal, Carlos Hamamé, Tomás Ossandón, Olivier Bertrand, Jean-Philippe Lachaux, Karim Jerbi

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Sarang S. Dalal · Juan R. Vidal · Carlos M. Hamamé · Tomás Ossandón · Olivier Bertrand · Jean-Philippe Lachaux · Karim Jerbi

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In their recent editorial, Nunez and Srinivasan (2010) assert that gamma band activity and intracranial recordings have been receiving an inordinate amount of attention in recent years. We agree that brain dynamics must be examined at all possible scales and across several frequency bands, and that it would be foolish to restrict our understanding of brain dynamics exclusively to intracranial recordings or higher frequency content. However, a number of points raised by the authors require further consideration.

How much emphasis is "too much"? A PubMed search of publications since 2007 reveals that the distribution of citations across frequency bands roughly follow their corresponding power distribution in the resting scalp EEG (see Figure 1), with 1,356 papers citing alpha or mu rhythms, while 790 cite gamma band activity and only 60 mention high gamma activity. Meanwhile, since 2007, 14,992 publications have cited EEG or MEG, while only 337 mention intracranial EEG[1].

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S.S. Dalal
Department of Psychology, Zukunftskolleg, University of Konstanz, Germany
MEG Department, CERMEP, Lyon, France
E-mail: sarang.dalal@uni-konstanz.de

S.S. Dalal, J.R. Vidal, C.M. Hamamé, T. Ossandón, O. Bertrand, J.-P. Lachaux, and K. Jerbi
INSERM U1028, CNRS UMR5292, Lyon Neuroscience Research Center, Brain Dynamics and Cognition Team, Lyon, France
Université Claude Bernard, Lyon 1, Lyon, France

1 Historical Emphasis on Low Frequencies

Clearly, reports of alpha rhythms and scalp EEG/MEG still dominate the literature. As Nunez and Srinivasan (2010) point out, there is an extremely large body of literature describing the association of low-frequency (<20 Hz) activity with a variety of brain states, clinical conditions, and cognitive responses. Perhaps this should provide even stronger motivation to scrutinize higher frequencies, to explore the relatively uncharted territory at the frontier of neuroscience, to complement what is already known about evoked responses and lower frequency oscillations. In fact, one major reason that higher frequencies had been virtually ignored for decades is simply because this activity was either assumed to be entirely noise and therefore systematically filtered out, or deemed incompatible with the traditional phase-locked evoked response model, even in intracranial recordings. Additionally, advances in both computer technology as well as analytical techniques were necessary to bring the analysis of higher frequency brain activity to the mainstream.

[1] search included: intracranial electroencephalography, electrocorticography, stereoelectroencephalography, depth electroencephalography, and subdural recordings. See supplementary material for precise PubMed search queries.

The assertion of Nunez and Srinivasan (2010) that beta and gamma frequencies are "largely absent at the scalp" is somewhat puzzling. Hans Berger himself carefully documented and named the beta rhythm of scalp EEG in his earliest works (Berger 1929, 1930), which were soon replicated by Tönnies (1934), Jasper and Carmichael (1935), and Jasper and Andrews (1938). In the decades since, an enormous volume of literature has proliferated with numerous diverse experiments describing robust beta modulations recorded with scalp EEG (to cite only a few, Tallon-Baudry et al. 2001; Pfurtscheller et al. 2001, 2005; Muthukumaraswamy and Johnson 2004; Parkes et al. 2006) and MEG (Salmelin et al. 1995; Gross et al. 2001; Cheyne et al. 2003; Jurkiewicz et al. 2006; Dalal et al. 2008; Engel and Fries 2010).

As for gamma band activity, Nunez and Srinivasan (2010) remind us of the technical challenges facing its reliable detection in scalp recordings. Certainly, gamma band activity may suffer some additional attenuation at the scalp due to summation of neighboring sources with incoherent phases (Pfurtscheller and Cooper 1975), but the skull and scalp do not inherently form a lowpass filter as the electrical properties of the various head tissues do not vary appreciably across the 0-100,000 Hz range (Oostendorp et al. 2000). Furthermore, we must emphasize that both experimental designs and analysis strategies have evolved to overcome poor signal-to-noise ratios (SNRs) – even when noise power is a thousand-fold greater than signal power in raw data – dramatically extending the usable bandwidth of electrophysiological recordings. Indeed, simple averaging across trials using raw data or band-limited power time courses decreases noise power in proportion to the number of trials acquired (Turetsky et al. 1988).

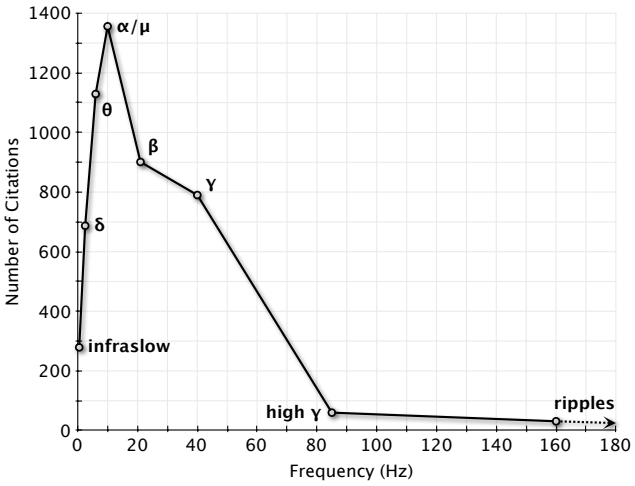

Fig. 1 EEG/MEG citations in PubMed since 2007, visualized as a spectrum across frequencies. Number of citations were plotted as a function of frequency band centers, using the following definitions. Infraslow: 0.01-1 Hz, δ: 1-4 Hz, θ: 4-8 Hz, α/μ: 8-12 Hz, β: 12-30 Hz, γ: 30-50 Hz, high-γ: 50-120 Hz, and ripples: 120-200 Hz.

2 Dissociating Cortical Gamma and Muscle Contamination

Electromyographic (EMG) interference contains significant power in the gamma band and thereby poses a challenge for resolving cortical gamma rhythms. Granted, this challenge may prove too formidable to allow noninvasive recordings to reliably detect gamma events in single trials. It may likewise hinder detection of transient pathological oscillations that may arise from relatively small generators, as might arise in epilepsy (Bragin et al. 2002; Tao et al. 2007; Wu et al. 2008). However, event-related paradigms benefit from repeated responses that can then be statistically analyzed across trials.

Whitham et al. (2007), who are cited as evidence casting doubt on the cortical origin of event-related gamma rhythms, in fact report a false *negative* rather than a false positive in their attempt to resolve scalp gamma modulations in the presence of ordinary background EMG. That is to say, muscular activity did not seem to produce significant *stimulus-locked* artifacts, but rather generated more continuous background noise that obscured task-induced gamma modulations. However, by subsequently inducing scalp muscle paralysis and thereby significantly reducing background noise levels, they found quite robust gamma modulations, confirmed in a follow-up study (Pope et al. 2009). These studies and others (Goncharova et al. 2003; Whitham et al. 2008) furthermore demonstrate that scalp EMG does in fact manifest most strongly close to scalp muscles, resulting in enhanced noise power along the periphery of an EEG cap but less intense centrally.

A more in-depth examination of the topography of task-related gamma modulations can provide clues as to whether they originate from cortex or artifactual sources such as the scalp muscles or eyes (Reva and Aftanas 2004; Trujillo et al. 2005; Yuval-Greenberg et al. 2008; Jerbi et al. 2009a). Principal component analysis (Mäki and Ilmoniemi 2011), independent component analysis (Keren et al. 2010), and some source localization algorithms based on spatial filters analytically formalize such spatial distinctions. Spatial filters, in particular, reconstruct source activity with what is essentially a weighted average across EEG/MEG sensors in addition to averaging across trials. This allows us to not only examine the spatially distinct sources of cortical activity versus artifact, but to boost effective

SNR as well (Sekihara et al. 2004; Ward et al. 1999; Väisänen and Malmivuo 2009). For even further sensitivity and generalizability, usually a large number of trials are acquired and statistics are computed across subjects. Indeed, these strategies seem to have the greatest success in resolving gamma activity at the scalp level (Dalal et al. 2008; Muthukumaraswamy 2010; Dockstader et al. 2010; Diwakar et al. 2011). Further confirmation on the possibilities and limitations of scalp recordings can be obtained from occasional opportunities to record them simultaneously with intracranial EEG (Dalal et al. 2008; Ball et al. 2009; Litvak et al. 2010; Rampp et al. 2010).

Given these considerations, our position is that there should be even *more* emphasis on gamma and beta, and researchers should take care not to filter this activity out upon acquisition, as any desired filtering for traditional analyses can now be easily done in post-processing software. Intracranial EEG, likewise, remains an underutilized technique to study human cognition, given the number of epilepsy surgery clinics around the world.

3 Intracranial EEG and Cortical Rhythms

Intracranial EEG (iEEG) in humans provides high-fidelity recordings of great clinical and research value. While intracranial recordings may occasionally be contaminated by eye muscle activity (Ball et al. 2009; Jerbi et al. 2009a; Kovach et al. 2011), these effects are predominantly restricted to recordings sites in the vicinity of the temporal pole and are efficiently reduced by using bipolar re-referencing strategies (Jerbi et al. 2009a). Certainly, these recordings are performed in patients with brain pathologies, so individual results are best interpreted in the context of converging evidence from other techniques; nevertheless, each patient's pathology tends to be different, therefore findings that remain consistent across patients can be regarded with reasonable confidence (Jerbi et al. 2009b).

The spatial coverage of iEEG is inherently limited, and the contribution of brain regions distant from the implanted zone cannot be reliably assessed. Nevertheless, a specific region of the brain is usually targeted for implantation based on a clinical hypothesis from scalp EEG/MEG, other neuroimaging techniques, and neurological or neuropsychological symptoms; any cognitive experiment tends to be targeted based on this coverage as well. Moreover, a sufficiently large volume of cortex must be activated to produce a recordable signal at the scalp (Cooper et al. 1965; Nunez and Srinivasan 2006), further raising the likelihood of detection by at least one intracranial electrode that would provide a partial validation of analyses from scalp recordings. Furthermore, source localization techniques similar to those applied to scalp EEG/MEG are under development for increasing the effective spatial sampling of iEEG (Dümpelmann et al. 2009; Axmacher et al. 2010). These techniques may be able to extend spatial coverage somewhat beyond the limits of the targeted brain volume. Finally, depth electrodes can access deeper brain structures such as the hippocampus (Ekstrom et al. 2005; Axmacher et al. 2010), thalamus (Sarnthein et al. 2003; Hanajima et al. 2004), and subthalamic nucleus (Litvak et al. 2010; Hirschmann et al. 2010), all of which play critical roles in brain function but are currently difficult or impossible to resolve with scalp recordings.

The earliest reports of subdural recordings in humans have shown activity across a range of frequencies, including the alpha band (Scarff and Rahm 1941; Jasper and Penfield 1949; Cooper et al. 1965). Numerous experiments in recent years have also shown task-related alpha modulations in subdural surface grids (Arroyo et al. 1993; Toro et al. 1994; Towle et al. 1995; Crone et al. 1998; Ohara et al. 2000; Crone et al. 2001; Brunner et al. 2005; Dalal et al. 2008; Blakely et al. 2009; Edwards et al. 2009; Swann et al. 2009; Fukuda et al. 2010), including centimeter-scale coherence (Shen et al. 1999; Aoki et al. 2001; Brunner et al. 2005). Tremblay et al. (2004) reported decreases of alpha band power over frontal and motor cortex not only with finger movements but with *observations* of finger movements. Furthermore, alpha modulations have been observed in depth EEG recordings as well (Dalal et al. 2009; Vidal et al. 2010). A procedure called hemicraniectomy, in which a portion of skull is removed while leaving the scalp and dura, can be considered similar to dural recordings; Voytek et al. (2010) found that the procedure intensifies modulations across a broad range of frequencies – including the alpha band – relative to intact scalp EEG. However, bipolar montages, often used in intracranial recording, may inherently obscure diffuse alpha activity. Clearly, large-scale phenomena, by definition, cannot be observed with the small spatial coverage available in many human iEEG studies, but most of the experiments cited here typically recorded over wide regions of cortex and consequently revealed widespread alpha modulations; many of these studies simultaneously analyzed gamma band modulations also, finding effects that were more task-specific as well as more focal spatially and temporally. (Jerbi et al. 2009b).

Let us not forget one of the primary goals of brain mapping, and the decisive motivation to record hu-

man intracranial EEG – to provide important diagnostic information for patient treatment. Here, too, analysis of intracranial gamma band activity has proven critical. Functional gamma mapping appears to correlate favorably with results of electrocortical stimulation mapping of eloquent cortex (Towle et al. 2008; Wu et al. 2010; Roland et al. 2010), and can be performed far more quickly and with less stress for the patient. While lower-frequency modulations may be seen along with gamma band enhancements, their spatial extent is often larger, reducing their usefulness for planning of resective surgery. Certain kinds of pathology (tumors, epileptogenic zones) also manifest themselves with abnormally high gamma-band power (Jacobs et al. 2010b) and coherence (Le Van Quyen et al. 1997). Finally, intracranial gamma band modulations frequently show higher spatial and functional specificity than other metrics, properties that are essential for real-time and brain-computer interface applications (Leuthardt et al. 2004; Lachaux et al. 2007b; Miller et al. 2009).

4 Plausible Role for Faster Rhythms in Binding, Neuronal Communication, and Inhibition

Slow oscillations may not provide a plausible mechanism for inherently fast integration processes, considering that neuronal interactions occur at a millisecond timescale. Singer (1993) specifically hypothesized that, "oscillations in the α- and β-frequency range would be too slow to serve as carrier signal for binding at this level of processing," especially if a few cycles of an oscillation are necessary, and proposed that the gamma range "appears as a good compromise between the opposing constraints to establish synchrony rapidly and with high temporal resolution on the one hand and over long distances on the other." However, the role of gamma rhythms in long-distance binding remains controversial (Kopell et al. 2000), especially with respect to visual processing, as recent studies have provided evidence against gamma-mediated binding in V1 (Ray and Maunsell 2010; Lima et al. 2010).

In parallel, the theoretical interpretations and foundations of gamma-band activity in cerebral networks have diversified beyond the binding hypothesis. Recent reviews have stressed the important mechanistic role of gamma activity regarding selective neural communication, neural plasticity, and neural activation and inhibition (Fries 2009). GABAergic interneurons form one of the largest cell populations in cortex and are known to operate largely in the gamma band, appearing to provide a key role in sensory gating (Cardin et al. 2009); a recent MEG study found that resting GABA concentration in the visual cortex of individual subjects predicts the gamma oscillation frequency induced by visual stimuli (Muthukumaraswamy et al. 2009). All of these potential implications compel further investigation of the gamma band alongside other frequencies, to explore aspects of perception and cognition that may not be accessible to other techniques.

Nunez and Srinivasan (2010) contend that studies of conscious perception during binocular rivalry using steady-state visual evoked potentials (SSVEPs) constitute the consciousness studies that are most closely related to perceptual binding. However, the hypothesis of binding by synchrony was conceived as a computational solution that could explain how a limited number of neurons, by means of their temporal coordination, may represent the enormous variability of the environment. In contrast, exogenously driving the cortical response through steady-state visual stimulation is highly useful for studying conscious perception (Srinivasan et al. 1999; Cosmelli et al. 2004). This frequency-tagging of active neural networks constitutes a powerful tool to investigate consciousness but does not necessarily explain the underlying mechanism by which consciousness arises.

5 Link between Gamma & BOLD

Accumulating evidence over the last decade suggests that investigations of gamma-band neuronal activity might be key to bridging the gap between fMRI and electrophysiological research. Numerous studies have established a tight relationship between increases in the blood-oxygenation level-dependent (BOLD) signal and task-related increases in broadband gamma ($\sim$30-150 Hz) of the LFP in humans (Mukamel et al. 2005; Nir et al. 2007; Lachaux et al. 2007a) and in animals (Logothetis et al. 2001; Niessing et al. 2005). By contrast, alpha-band modulations often seem to be negatively correlated with simultaneously recorded BOLD responses (e.g., Laufs et al. 2003; Moosmann et al. 2003) but more spatially distributed.

A further indicator for the specificity of the coupling between gamma-band power and BOLD comes from recent reports indicating that positive and negative BOLD responses are associated respectively with increases and decreases of broadband gamma power in the primary visual cortex of monkeys (Shmuel et al. 2006). More recently, the coupling between negative BOLD responses and suppression of gamma power has also been suggested by direct electrophysiological recordings in the so-called *default-mode network* known to display BOLD deactivations during attention-demanding tasks.

Several studies by our group and others show that execution of externally oriented attention-demanding tasks leads to suppressions of broad-band gamma power in specific default-mode network structures (Hayden et al. 2009; Lachaux et al. 2008; Ossandón et al. 2009; Jerbi et al. 2010). Therefore future studies of broadband gamma should improve our understanding of the neurophysiological basis of the BOLD signal and advance our understanding of the functional role of large-scale intrinsic networks such as the default-mode network.

6 Final Words

The term "gamma band" as currently used represents a very broad range of frequencies that likely encompasses a few different neural mechanisms, and we support Nunez and Srinivasan (2010) in cautioning against the temptation to rely on it as a "catch-all category." The literature describing epilepsy-related high frequency oscillations has recognized some differences across this range, using the term *ripples* to describe activity between about 80-200 Hz but distinguishing them from "fast ripples" that appear to represent a distinct phenomenon between 250-500 Hz (Bragin et al. 1999). In the cognitive domain, more differentiation needs to be made between, for example, 40 Hz narrowband oscillations and broader 70-120 Hz power enhancements (Vidal et al. 2006; Hoogenboom et al. 2006; Wyart and Tallon-Baudry 2008; Crone et al. 2010), or even higher frequency phenomena of about 130-250 Hz (often also referred to as ripples) in the hippocampus and entorhinal cortex (Axmacher et al. 2008; Le Van Quyen et al. 2010) and 600 Hz somatosensory evoked potentials (Curio et al. 1994). A more nuanced view of these high frequencies should be considered, particularly in light of a recent study demonstrating the specificity of different subbands across the 60-500 Hz range to various cognitive tasks (Gaona et al. 2011). As suggested by Curio (2000) and Jacobs et al. (2010a), perhaps the EEG/MEG community should agree on more specific, consistent terminology to better differentiate the various high-frequency phenomena in the literature. In fact, if such distinctions were made, one could argue that alpha actually attracts a rather disproportionate amount of attention for encompassing only 4 Hz of the spectrum!

Figure 1 suggests that very low frequency phenomena (below 4 Hz) such as the slow cortical potential (Birbaumer et al. 1990; He et al. 2008) or infraslow fluctuations (e.g., Monto et al. 2008), as well as delta-band frequencies (e.g., Jerbi et al. 2007) may also deserve more studies and further evaluation. Ultimately, a more complete view of brain dynamics and cognition must come from examining activity across a broad range of frequencies. As Nunez and Srinivasan (2010) point out, cross-frequency interaction may provide a mechanism for inter-network communication during cognitive processing, and already studies on cross-frequency interaction from several laboratories have been rapidly elucidating the interplay between frequency bands (Canolty et al. 2006; Jensen and Colgin 2007; Monto et al. 2008; Osipova et al. 2008; de Lange et al. 2008; Jerbi and Bertrand 2009; Le Van Quyen et al. 2010; Dalal et al. 2010; Canolty and Knight 2010). It is therefore clear that the neural correlates of cognition are not confined to a specific frequency band and that the big picture can only be achieved by putting the pieces of the puzzle back together, i.e., not only including all frequencies of the spectrum but also various measures of brain responses across multiple spatial scales.

We shall also conclude with inspiration by Jacobs (2010), who notes that so much valuable information has been gained from simply opening up filters, using faster sampling rates, and examining the full frequency spectrum in subsequent analyses; indeed, her editorial closes with optimism that ever higher frequency activity reflecting ever earlier responses will arise from technical advances, not to the exclusion of lower frequency correlates, but rather in the context of them, and we couldn't agree more.

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